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Review

A review of tribe Indigofereae (Leguminosae–Papilionoideae) in Southern Africa (including South Africa, Lesotho, Swaziland & Namibia; excluding Botswana)

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ABSTRACT

A review is given of the legume tribe Indigofereae for the region of southern Africa including Namibia. The overall distribution, taxon statistics, phylogenetic relationships, uses, bibliography and a checklist of taxa in the tribe are provided covering the c. 340 taxa of Indigofereae within the region.

Contents

1. Introduction

The Indigofereae is a small tribe comprising six genera of often very attractive, pink to red-flowered shrubs and herbs. They are mostly African–Madagascan in distribution, except for the largest genus *Indigofera* which is pantropical. *Indigofera* is the third largest genus in Leguminosae, with 75% of the c. 750 species restricted to Africa–Madagascar, while the Sino-Himalayan region, Australia and the two neotropical centres of Mexico and the Paraná of SE South America are other nuclei of species diversity (Schrire et al., 2009; Ferretti et al., 2012).

Indigofereae is well resolved as sister to a large clade comprising tribes Millettieae, Abreae, Phaseoleae, Desmodieae and Psoraleeae (Wojciechowski et al., 2004; Schrire, 2005; Schrire et al., 2009; Cardoso et al., 2012; LPWG, 2013). The tribe is well supported as a monophyletic group sister to the Madagascan dry forest genus *Disynstemon* (Schrire et al., 2009), with *Phylloxylon* (7 spp.), also endemic to Madagascar, being strongly resolved as the earliest diverging clade within Indigofereae. Sister to *Indigofera* is the well supported CRIM clade (Schrire, 1995; Barker et al., 2000; Schrire, 2005; Schrire et al., 2003, 2009) comprising the genera *Cyamopsis* (4 spp.), *Indigastrum* (9 spp.), *Microcharis* (36 spp.) and *Rhynchotropis* (2 spp.).

2. Phylogeny, biogeography and uses

In the analysis of Schrire et al. (2009), the age of the stem clade of the tribe was fixed by both the maximum (55 Ma) and minimum (50 Ma)

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age estimates of Indigofereae, as reported by Lavin et al. (2005). The respective crown clade ages in Schrire et al. (2009) are c. 33 Ma for Indigofereae, c. 27 Ma for the CRIM–*Microcharis* clade, c. 23 Ma for *Indigofera*, and for the oldest two clades in *Indigofera*, c. 22 Ma for the Cape clade and 15.5 Ma for the Tethyan clade. This analysis also showed that much of the extant diversification of Indigofereae took place within the last 16 Ma, implicating dispersal as the dominant explanation for the worldwide distribution of *Indigofera*.

All species of *Indigofera* comprise just four main clades, each diagnosable by morphological synapomorphies and ecological and geographical predilections (Barker et al., 2000; Schrire et al., 2003, 2009). This suggests niche conservation (ecology) and dispersal limitation (geography) are important processes shaping the Indigofereae phylogeny in different biomes (Schrire et al., 2005a,b). The Cape (c. 110 spp.) and Tethyan (c. 150 spp.) clades of *Indigofera* are, in addition to being the oldest of the four, also the only clades optimized as originating in the semi-arid Succulent Biome. Clades confined to temperate and succulent-rich biomes are more dispersal limited and show more geographical phylogenetic structure than those inhabiting tropical rainforest and savanna (grass) biomes (Schrire et al., 2005a,b).

Phylogenetic structure of traits within each of the four clades of *Indigofera* is exemplified by different suites of morphological and chemical characters associated with plant defenses (Schrire et al., 2009). The large divergence of defensive strategies evident among the four *Indigofera* clades suggested that herbivores and pathogens have imposed strong selection pressures on *Indigofera* species. A remarkable finding was that the Tethyan and Pantropical (c. 305 spp.) clades listed the largest number of toxic and medicinally used species in the genus respectively, owing to their complex chemistry. The Palaeotropical clade (c. 185 spp.), however, with its relatively simple chemistry and reliance on ant-association defences, hosted the largest number of good quality animal feed species.

Indigofera comprises a significant group of economically important indigo dye-producing species (Gillett, 1958; Burkill, 1995), as well as many ecologically sensitive taxa that show remarkable specificity to habitat, for which they are valuable indicators. The genus also contains many important pasture legumes that occupy an extremely wide range of different habitats across the whole southern African region. The high number of species in the genus attests to a remarkable ability to diversify into almost every seasonally dry habitat, and it is not unusual to find a number of different sections of the genus represented in any one ecological community. It is an excellent model genus for exploring the relationships between ecology and systematics exemplifying, as it does, the broadest of geographical and ecological amplitudes within Southern Africa.

3. Taxonomy and bibliography

The historical development of botanical discovery of the tribe in southern Africa is summarised in Table 1 (*Indigofera*) and Table 3 (*Cyamopsis*, *Indigastrum* and *Microcharis*). These tables are arranged as a chronology of authors (of basionyms), and treatments describing currently recognised species. A summary of statistics of taxon numbers in *Indigofera* is given in Table 2, and for the other three genera in Table 4. Subgenera, sections, subsections and currently recognised species and infraspecific taxa (with synonymy) are listed in Appendix 1 (*Indigofera*), and in Appendix 2 (*Cyamopsis*, *Indigastrum and Microcharis*). The Namibian flora comprises *Cyamopsis* (2 spp.), *Indigastrum* (6 spp. including 1 new species), *Microcharis* (2 spp.) and *Indigofera* (55 spp. including 4 new species). *Indigastrum* (2 spp.) and *Indigofera* (21 spp.) are either

Table 1
Chronology of authors (of basionyms) and treatments, describing currently recognised species of southern African *Indigofera*.

Date	*Indigofera* in southern Africa (author/treatment of currently recognised spp. based on basionym).	No. of S. Afr. spp. described
1753–1760	Linnaeus C.; 4 in Sp. Pl. 2.; 1 in Plant. Rar. Afric., no. 33	5
1768	Burman, N.L., f.; 1 in Prod. Fl. Cap.; 1 in Fl. Ind.	2
1771	Linnaeus C.; Mant. Pl.	3
1775	Forsskal P.; Fl. Aegypt. -Arab.	1
1781	Linnaeus C., f.; Suppl. Pl.	7
1789	Aiton W.; Hort. Kew. 3.	2
1789	Jacquin N.J.; Coll. Bot. 2.	1
1800	Thunberg C.; Prod. Pl. Cap.	6
1814	Desvaux N.A.; Journ. Bot., Paris, ser. 2, 3.	1
1822–1827.	Sprengel, K.; 1 in Neu. Entdeck. 3.; 2 in Syst, Veg. 4.	3
1825	Candolle, A.P. de; Prod. Syst. Nat.	7 (*38 spp. described before 1830*)
1836 (Jan.)	Ecklon C. & Zeyher C.; Enum. Pl. Afr. Austr.; treatment of 66 Cape species in 3 sections	23
1836 (Feb.)	Meyer, E.; Comm. Pl. Afr.; treatment of 73 Cape & Natal species in 7 sections.	20
1856	Jaub. & Spach; Ill. Pl. Orient. 5.	3
1862	Harv., Fl. Cap. 2 (many as Benth. ex Harv.); treatment of 115 Cape and Natal species in 2 subgenera & 8 sections	20
1871	Baker J.G.; Fl. Trop. Afr. 2.	7
1883–1887	Baker J.G.; J. Linn. Soc., Bot. 20 & 22.	2
1888–1889	Schinz H.; 2 spp. in Verh. Bot. Ver. Prov. Brand. 30.	3
1893–1903	Harms H.; Warb., Kunene-Samb.-Exped. Baum; in Kuntze, Rev. Gen. Pl. 3(2).	2
1896–1906	Bolus H.; 4 spp. in Journ. Bot. 34.	5
1897–1899	Schlechter R.; Engl. Bot. Jahrb. 24 & 27; J. Bot. 35.	3
1903–1926	Baker E.G., f.; 9 in Mitt. Bot. Mus. Univ. Zurich 22; 2 in Leg. Trop. Afr.	11
1915	Bolus L.; Ann. Bol. Herb. 1; Ann. S.Afr. Mus. 9.	2
1921	Burtt Davy J.; Bull. Misc. Inform., Kew	2
1925	Brown, N.E.; Bull. Misc. Inf. Kew	22
1926–1932	Brown, N.E.; in Burtt Davy J., Man Fl. Pl. Tvl. 1 & 2; Treatment of 82 Transvaal & Swaziland species.	9
1932	Fourcade H.; Trans. Roy. Soc. S. Afr. 21	3
1958	Gillett J.B., Kew Bull., Add. Ser. 1; tropical African *Indigofera* in 3 subgen. (excl. *Indigastrum* & *Microcharis*), 2 sect., 17 subsect. in sect. *Indigofera*; including 63 S. Afr. spp.	3
1951–1957	Merxmueller H.; Mitt. Bot. Staatss. München 1; Bull. Jard. Bot. Brux. 27.	2
1960	Torre A.; Mem. Junta. Invest. Ultram. ser. 2, 19.	2
1970	Schreiber A.; Mitt. Bot. Staatss. München 8.	3
1982–1987	Stirton C.H.; 2 with Jarvie J.K. in Bothalia 17	3
1997–2012	Schrire B.D.; Curtis's Bot. Mag. 14; 2 in Fl. Zamb. 3(4).	3
Authors describing 1 sp. each: 1813, Poir.; 1839, Walp.; 1843, Meisn.; 1847 A. Rich.; 1861, Klotzsch; 1895, Taub.; 1905, A. Zahlbr.; 1909, Diels; 1922, Dinter; 1986, Hilliard & Burtt; 1992, P. Phillipson.		11

Table 2
Summary statistics of taxon numbers in southern African *Indigofera*.

202 currently recognised species of southern African *Indigofera* have been described to date.
c. 70 new species are still to be described and 9 new combinations to be made.
In total 272 spp. (and 2 cultivated spp.) are recognised for the southern African flora region (including South Africa, Lesotho, Swaziland and Namibia) of which 55 spp. occur in Namibia
213 spp. are endemic to the region (78%) and 8 spp. to Namibia (15%)
21 currently recognised infraspecific taxa (12 subspp. and 9 vars.) have been previously described.
26 new infraspecific taxa (15 subspp. and 11 vars.) are still to be described.
In total 47 infraspecific taxa are recognised in *Indigofera* (27 subspp. and 20 vars).
In total c. 321 taxa of *Indigofera* occur in the flora area.
18 sections and 4 subsections are currently recognised, with 5 new sections and 7 new subsections yet to be described.
In total *Indigofera* comprises 23 sections and 11 subsections in this latest circumscription of the genus in Southern Africa.

Table 3
Chronology of authors (of basionyms) and treatments, describing currently recognised species of *Cyamopsis*, *Indigastrum* and *Microcharis* in southern Africa.

Date	*Cyamopsis*	No. of S. Afr. spp. described
1767	Linnaeus C.; Mant.	1 (introduced)
1832	Guill. & Perr., Fl. Seneg. Tent.	1
1888	Schinz, Abh. Bot. Ver. Brand. 30	1
	Indigastrum	
1832	Guill. & Perr., Fl. Seneg. Tent.	1
1834	Heyne ex Wight & Arn., Prodr. Pl. Penins. Ind. Or.	1
1826	Spreng., Syst. Veg, ed 16, 3.	1
1836	Meyer, E.; Comm. Pl. Afr.	2
1862	Harv., Fl. Cap. 2	1
1922	Dinter K.; Feddes Repert. 18	1
1960	Torre A.; Mem. Junta Invest. Ultram. ser. 2, 19.	1
	Microcharis	
1865	Benth., Trans. Linn. Soc. 25	1
1897	N.E.Br., Bull. Misc. Inform., Kew	1
1936	Milne-Redhead E.; Bull. Misc. Inform., Kew.	1
1955	Gillett J.B.; Kew Bull. 1955	1

endemic to Namibia, or also occur north of (but outside) the rest of the flora area (and can thus be discounted from the total species number of the flora area if Namibia is excluded). Botswana is not included in this region as the area is already covered for Flora Zambesiaca (Schrire, 2012).

Appendices: Checklist of southern African Indigofereae

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.sajb.2013.06.014.

Table 4
Summary statistics of taxon numbers in *Cyamopsis*, *Indigastrum* and *Microcharis* in southern African *Indigofera*.

Cyamopsis
3 species (1 an introduced food crop); no infraspecifics. No endemics in flora area.
Indigastrum
9 species, 8 currently recognised with 1 new species still to be described; 6 spp. endemic to flora area (67%)
1 new subgenus to be described
3 subspp. recognised within 2 species
Microcharis
4 species recognised, 1 typical subsp. the only infrageneric taxon recognised to date. No endemics in flora area.
1 new var. yet to be described.

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